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Short Communication

A preliminary framework to model wing polyphenism in aphids threatened by predators

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Abstract

In this study, we integrate population theory with experimental data from the literature and from our laboratory experiments to develop a preliminary predator–prey model. This model investigates wing polyphenism in aphids exposed to predators. We propose a system of three ordinary differential equations to simulate interactions among apterous aphids, alate aphids, and their predators. Although essential for biocontrol, predators can induce wing development, enabling aphids to disperse to previously uninfested plantations. Building on the work of Sentis et al. (2019), who found that ladybug presence increases winged offspring production (an effect dependent on the host plant) in *Acyrthosiphon pisum*, with stronger responses in alfalfa-specialized lineages than in clover-specialized ones, we investigated how host plant type shapes aphid responses using an analogous system with *Myzus persicae* on broccoli (a favorable host, akin to alfalfa for a strong response) and basil (a repellent host, akin to clover for a weak response). Our model results indicate that predator presence promotes alate formation, a response modulated by the predator's attack rate, its conversion efficiency, and host plant effects, as plants vary in their attractiveness to different aphid morphs.

Key words: Interactions, mathematical model, phenotypic plasticity

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Introduction

Polyphenism is a form of developmental plasticity that allows a single genotype to produce different phenotypes in response to environmental cues such as temperature, diet, and predator threat (Srinivasan and Brisson 2012). Widespread among arthropods, aphids are a classic example, in which a single genetic blueprint can yield vastly different forms to enhance survival (Simpson et al. 2011). For instance, wingless (apterous) aphids invest in producing winged (alate) offspring to escape ladybird predation (Shuo et al. 2020). This transgenerational shift toward a dispersing morph safeguards the lineage by facilitating escape from immediate danger, triggered by cues such as alarm pheromones or physical disturbance (Shuo et al. 2020).

This scenario creates a complex challenge for biological control. While predators are vital for managing aphid populations (Valentini et al. 2025),

they can inadvertently trigger the dispersal of alate aphids to new, unaffected areas (Feng et al. 2004; Hodgson et al. 2005). Understanding this dynamic is therefore critical for designing effective and sustainable pest management strategies.

Sentis et al. (2019) experimentally evaluated this transgenerational phenotypic plasticity in *Acyrthosiphon pisum* (Hemiptera: Aphididae) in response to *Harmonia axyridis* (Coleoptera: Coccinellidae), asking whether the response varied between lineages specialized on alfalfa vs. clover. Their results support intraspecific variation in predator-induced plasticity, with alfalfa-specialized lineages showing a stronger response than clover-specialized ones. The authors suggest that host plant specialization may shape herbivore responses to predators within a tri-trophic context. While Sentis et al. (2019) focused on *A. pisum* lineages specialized on alfalfa (strong plastic response) vs. clover (weaker response), we draw an analogy in this study using *Myzus persicae* (Hemiptera: Aphididae) on broccoli (a favorable host promoting high densities and strong induction potential, similar to alfalfa) and basil (a less favorable host leading to low densities and weak induction, similar to clover), acknowledging that direct equivalence is not implied due to species and plant differences. Motivated by these findings, we propose a preliminary predator–prey model to investigate winged aphid polyphenism, analogously adapting the host plant–modulated response to our system with *M. persicae*, specifically examining how increased predator density elevates the probability of alate production.

Methods

Mathematical model

The approach presented in this study provides conditions for implementing a deterministic tri-trophic population dynamics model, formulated as a system of three ordinary differential equations (ODEs). It simulates the interactions among apterous aphids (A_p), alate aphids (A_l), and predators (P). The objective is to analyze phenotypic plasticity in response to polyphenism induced by predation and modulated by host plant type. The model captures the essence of the experimental findings of Sentis et al. (2019), who demonstrated that pea aphid (*A. pisum*) lineages exhibit transgenerational phenotypic responses, with variation linked to host plant biotypes (stronger on alfalfa than on clover). We analogously incorporate this variation by using *M. persicae* growth rates on broccoli (akin to alfalfa, a favorable host) and basil (akin to clover, a repellent host). Our model extends a classic predator–prey framework (e.g., Lotka–Volterra with a type II functional response) by partitioning the aphid population into apterous and alate forms, with the latter subject to emigration as an escape mechanism.

The state variables are A_p: density of apterous aphids; A_l: density of alate aphids; and P: density of predators, ladybirds in the present study. The model simulates over a specified time horizon (here, 0–500 time units, given in days) with initial conditions A_p: = 20, A_l: = 5, P = 2. Parameters are defined in a list (parameter base) for flexibility. The output is visualized as time-series trajectories to illustrate dynamic relationships.

Model parameters

The intrinsic growth rates were experimentally estimated (see the section *Aphid growth rate experiments*). The remaining parameters were assigned the following values to explore polyphenism in the simulations while ensuring specific ecological conditions:

- K (carrying capacity) = 30: set to prevent aphid densities from reaching levels capable of triggering crowding-induced polyphenism;
- a (attack rate) = 0.1: the minimum value required to trigger predator-induced polyphenism;
- e (predator conversion efficiency) = 0.01: a baseline value for investigating polyphenism;
- d (predator mortality rate) = 0.01: a minimum value to account for predator mortality;
- μ (natural aphid mortality rate) = 0.01: a minimum value to account for mortality from factors other than predation;
- h (handling time) = 0.02: the minimum value required to ensure a type II functional response;
- m (apterous aphid emigration rate) = 0.1: set to ensure at least 10% emigration in response to polyphenism.

Equations and functions

The model computes the rates of change for A_p, A_l, and P at each time step (Equations 1, 2, and 3). It employs a type II functional response for predation to account for predator saturation at high prey densities. The dynamic equations are written as follows:

$$\frac{dA_p}{dt} = rA_p\left(1 - \frac{A_p + A_l}{K}\right)(1 - pr) - \mu A_p a_r P A_p \quad (1)$$

The logistic growth is given by $rA_p\left(1 - \frac{A_p + A_l}{K}\right)(1 - pr)$, where r is the intrinsic growth rate for apterous aphids, K is the carrying capacity shared by A_p, and A_l, and (1 − pr) determines the fraction of reproduction allocated to apterous offspring (the remainder to alates via polyphenism). The term − μA is the natural aphid mortality per-capita rate, and the predation is structured by $a_r P A_p$, where a_r (attack rate) is per-predator, per-prey attack rate, density dependent via the type II functional response. Apterous aphids grow logistically but divert reproduction to alates under threat (via pr), suffer background mortality, and are consumed by predators.

$$\frac{dA_l}{dt} = rA_p\left(1 - \frac{A_p + A_l}{K}\right)pr + r_l A_l\left(1 - \frac{A_p + A_l}{K}\right) - \mu A_l a_r P A_l - mA_l \quad (2)$$

The term $rA_p\left(1 - \frac{A_p + A_l}{K}\right)pr$ determines the induced production from apterous aphids, where pr is the probability of producing alates, diverting reproduction from A_p, The alate intrinsic growth rate, which is given by r_l (here equal to r), and $-\mu A_l$ the mortality, the same as for apterous aphids. Predation is determined as $a_r P A_l$, assuming alates are equally vulnerable, although they may

escape via flight. Emigration is $-mA_l$, a constant per-capita rate representing dispersal of alate forms. Alates are produced via polyphenism from apterous mothers, grow logistically, suffer mortality and predation, and emigrate, reflecting their adaptive role in escaping threats from predators.

$$\frac{dP}{dt} = ea_r P\left(A_p + A_l\right) - dP \tag{3}$$

The expression $ea_rP\ (A_p + A_l)$ gives predator growth from consumption of aphids, where e is the conversion efficiency (the proportion of consumed aphids converted into predator biomass), and total aphids ($A_p + A_l$) are the prey pool. The term $-dP$ is the predator per-capita death rate. Predators grow by consuming both aphid morphs, with density-dependent efficiency via a_r, and decline due to natural mortality.

Auxiliary functions

Functional response

The attack rate (a_r) is applied to the wing aphid polyphenism model to determine the type II functional response as $\frac{a}{[1 + h\left(A_p + A_l\right)]}$, where a is the maximum attack rate *per* predator and h is the handling time, reducing the rate at high prey densities.

Polyphenism probability

We estimated the polyphenism probability (pr)—the likelihood of apterous aphids producing alate offspring under predator threat—based on data from Sentis et al. (2019).

We approximated the linear relationship they observed (predator effect on alate proportion regressed against effect on aphid density) and analogously applied it to our model using *M. persicae* growth rates on broccoli (a favorable host promoting higher densities, akin to alfalfa for potentially stronger responses) and basil (a repellent host leading to lower densities, akin to clover for weaker responses). This adaptation is indirect, as our experiments tested plant repellency effects on growth rates in the absence of predators; thus, the host-modulated polyphenism is simulated rather than empirically validated in our system. Direct equivalence is not implied due to species and plant differences.

The approximation was performed by using the instantaneous density reduction term $\frac{-a_rPA_p}{20}$ as a proxy for the x-axis. We then defined $pr_{calc} = 0.3 - 0.0003\left(\frac{-a_rPA_p}{20}\right)$ to capture the positive induction trend, with values clamped between 0 and 0.3 to align with the empirical bounds observed in Sentis et al. (2019). The decreasing regression line shown in our Fig. 1 was adapted from the relationship illustrated in Fig. 4 of Sentis et al. (2019). The denominator (20) scales the predation term to our initial apterous population conditions.

In our study, the function pr_{calc} mirrors the linear relationship investigated by Sentis et al. (2019), specifying it to the broccoli system (analogous to alfalfa), experimentally investigated with aphid growth rates, and the basil system (akin to clover with weak response), analyzing the influence of its repellency on aphid growth rates. The adaptation to a continuous-time model simplifies the paper's 10-day transgenerational experiment (wingless mothers producing winged offspring)

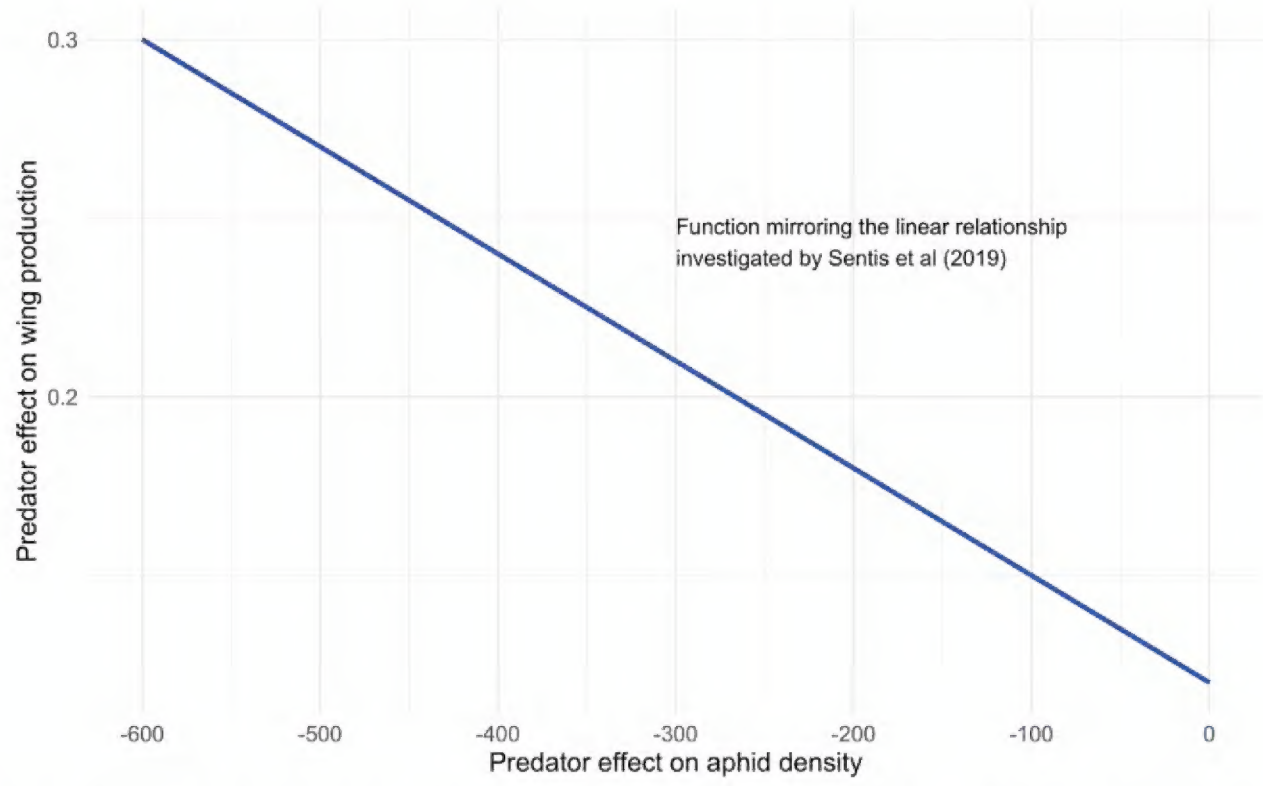

Figure 1. Linear relationship between the suppressive effect of predators on aphid population density (x-axis) and their effect on the proportion of winged aphids (y-axis). Adapted from fig. 4 in Sentis et al. (2019), showing only the decreasing linear trend. Original figure © Sentis et al. (2019), licensed under Creative Commons Attribution 4.0 International (CC BY 4.0) (https://creativecommons.org/licenses/by/4.0/; https://doi.org/10.1038/s41598-019-45220-0).

while preserving the essence: predator presence induces polyphenism, modulated by plant specialization. This matches the paper's emphasis on intraspecific variation in plastic responses and its potential evolutionary link to host-plant adaptation.

Bifurcation diagram

A bifurcation diagram illustrates how a system's long-term behavior changes quantitatively and qualitatively as a parameter is varied, revealing thresholds for transitions between stable states, oscillations, or chaos (Troost et al. 2007). While our preliminary analysis of the model's dynamics did not reveal complex cycles or chaos, we use bifurcation analysis here primarily for sensitivity analysis. We explore the parameter space of the predator's attack rate (a) and conversion efficiency (e) to identify ranges that strongly induce alate formation.

Bifurcation diagrams are key for analyzing predator–prey systems with polyphenism, as they illustrate how shifts in parameters such as attack rate and conversion efficiency can cause major qualitative and quantitative changes in population dynamics, highlighting thresholds for stability, collapse, or outbreaks. They are vital for understanding how predator presence drives polyphenism, showing how these parameters, alongside factors such as fear-induced behaviors, influence system stability and lead to complex dynamics or shifts between population states.

Numerical simulation and bifurcation analysis of aphid–predator dynamics

The polyphenism model was implemented using the deSolve package in R (R Core Team 2023), with the ode() function employing the lsoda integrator to solve a system of ordinary differential equations (ODEs). A bifurcation analysis was conducted by varying the predator conversion efficiency (e) and the attack rate (a_{γ}), iterating simulations to record equilibrium aphid densities (apterous and alate).

Aphid growth rate experiments

We conducted greenhouse experiments to estimate intrinsic growth rates (r) of *M. persicae* on broccoli (a favorable host promoting higher densities, akin to alfalfa in Sentis et al. (2019) for potentially stronger polyphenism responses) and basil-intercropped broccoli (a repellent host leading to lower densities, akin to clover for weaker responses). This provides model parameters to simulate indirect host plant effects on polyphenism induction, analogous to host specialization in Sentis et al. (2019), although our trials did not include empirical predator exposure.

We performed greenhouse trials at the ESALQ/USP Department of Entomology and Acarology, Piracicaba, Brazil, using a randomized block design with two treatments: (1) broccoli grown alone and (2) broccoli intercropped with basil. Each broccoli plant served as a sampling unit, with 10 replicates per block, for a total of 20 per treatment. Broccoli plants, 25 cm tall and spaced 5 cm apart, were planted in a single row. Basil plants were arranged in parallel rows behind the broccoli, spaced 5 cm apart and set 2 meters apart per treatment.

We placed three adult apterous *M. persicae* (Hemiptera: Aphididae) on each broccoli plant under greenhouse conditions averaging 32.5 °C/21 °C (max/min temperature) and 96%/40% (max/min humidity). After 72 hours, the total number of aphids (adults and nymphs) per broccoli plant was recorded. We estimated the intrinsic rate of increase (Culliney and Pimentel 1985), $r\,(apterous)$ and $r_l\,(alates)$ in the current study, applying the same value for r and r_l according to the following equation $r\,(or\,r_l) = \frac{ln\left(\frac{N_{X+1}}{N_X}\right)}{t}$. The mean intrinsic growth rate was used in Equations (1) and (2), resulting in $r_{broccoli} = 0.31 \pm 0.58$ (SD) and $r_{basil} = -0.16 \pm 0.92$ (Carvalho et al. 2025). A mixed linear model showed that basil presence significantly lowered the intrinsic population growth rate (p = 0.0375). Despite high variability in these estimates (e.g., SD exceeding the mean for broccoli, likely due to environmental factors such as temperature or aphid clonal differences), the positive r on broccoli and negative r on basil consistently reflect favorable vs. repellent host effects.

Results and discussion

Fig. 2 illustrates the impact of predator presence on alate induction. Panel A shows the scenario without predators, where apterous aphids predominate and alates go extinct quickly due to the lack of an induction cue. Panels B and C demonstrate that predation induces alate production, with differences emerging from varying predator conversion efficiencies (e). Although the population sizes of apterous and alate aphids appear similar initially, the model shows that predation leads to a sustained alate population approximately twice the size of the apterous population, highlighting the polyphenic response.

This aligns with general discussions on polyphenism triggers (Dixon 1998; Gilbert 2001; Simpson et al. 2011) and the specific mechanisms—including predator presence—outlined by Srinivasan and Brisson (2012). Panel D shows the repellent effect of basil in an intercrop, driving both aphid populations to extinction and, consequently, eliminating the predator population, a phenomenon supported by Khan et al. (2024).

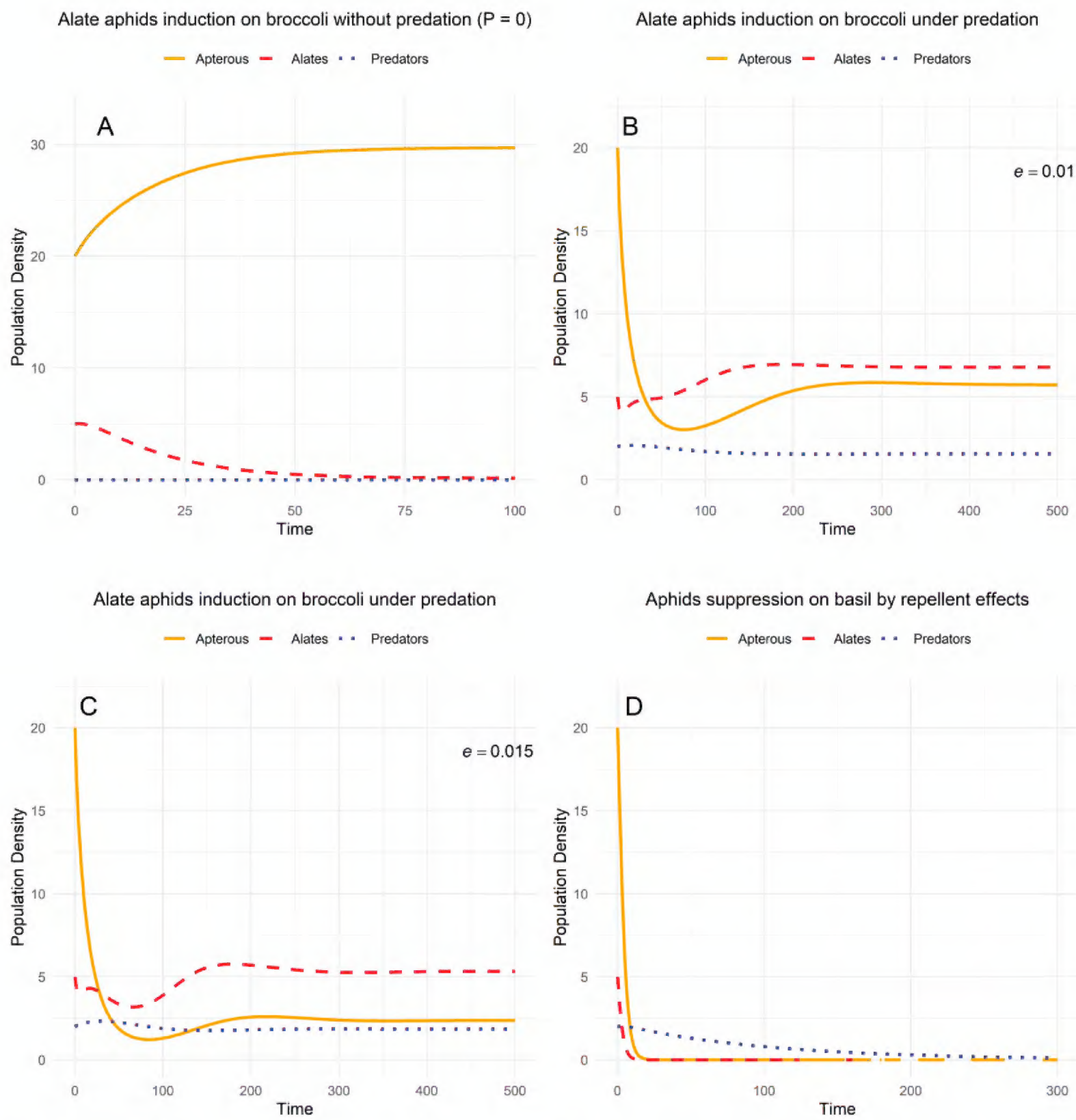

Figure 2. Alate aphid induction under different conditions: **A.** On broccoli without predation; **B.** On broccoli with predation using a predator conversion efficiency of 0.01; **C.** On broccoli with predation using a predator conversion efficiency of 0.015, and **D.** On a broccoli–basil intercrop. Panels illustrate population trajectories of apterous and alate aphids and predators over 500 time steps.

Our key empirical foundation is the work of Sentis et al. (2019), which demonstrated the transgenerational plasticity we model in *A. pisum* on alfalfa versus clover. By analogy, our results with *M. persicae* on broccoli (strong response, akin to alfalfa) and basil (weak response, akin to clover) are consistent with the differences between the plants investigated in Sentis et al. (2019).

Fig. 3 presents bifurcation diagrams analyzing the influence of predator conversion efficiency (e) and attack rate (a) on alate production. In Fig. 3A, aphid populations decline for $0 < e < 0.1$, followed by a peak where alates exceed apterous aphids. Fig. 3B shows a similar decline for $0 < a < 0.35$, with alates peaking just before $a = 0.3$. The attack rate and conversion efficiency are pivotal parameters in predator–prey dynamics (Hassell 1978; Beltrà et al. 2018), especially in systems with polyphenism (Mougi and Kishida 2009). The attack rate (a) determines predation pressure and directly drives aphid decline, while conversion efficiency (e) determines how effectively consumed aphids fuel predator population growth (Li and Montagnes 2015; Tamashiro et al. 2023). Together, these

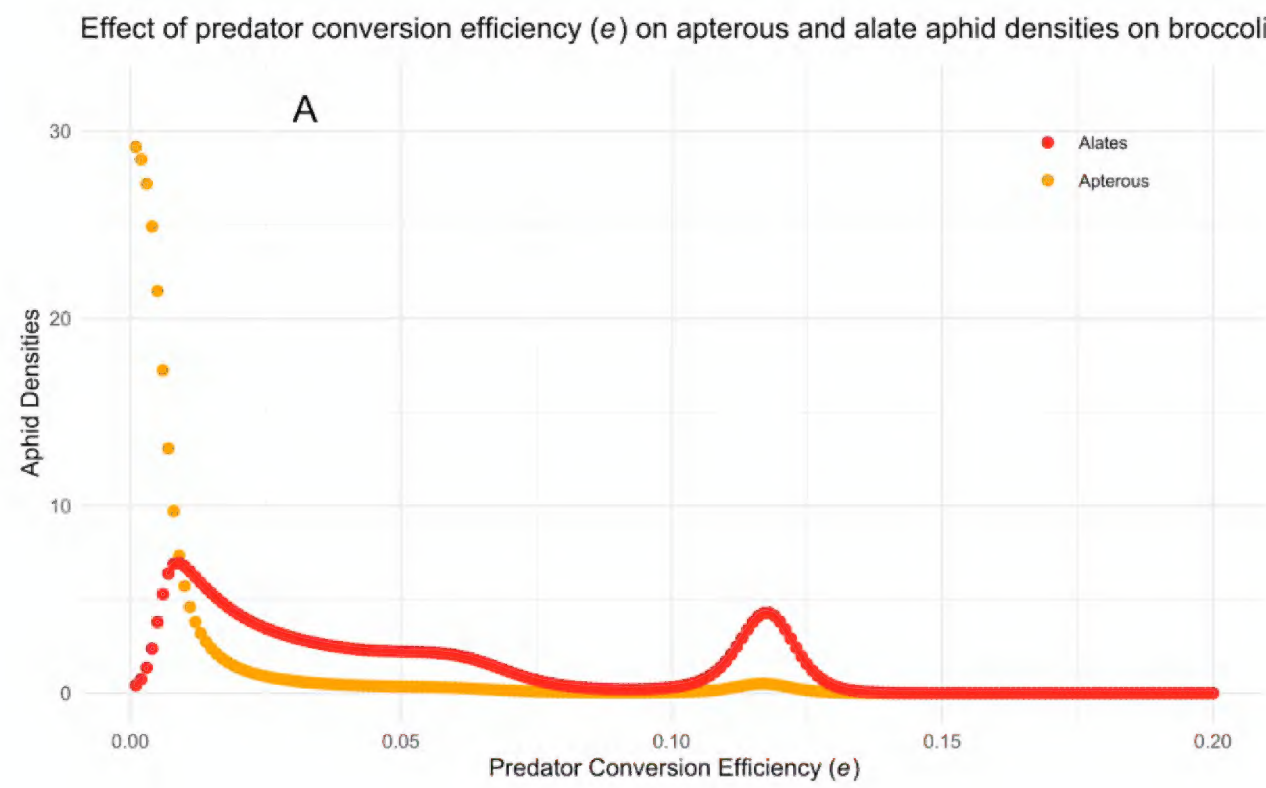

Figure 3. Bifurcation diagram showing the influence of predator conversion efficiency (e) **A.** And attack rate (a); **B.** On alates and apterous on broccoli.

parameters critically influence population stability and are key to understanding systems where alate production is a plastic response to predation.

This proposal certainly has limitations, particularly the lack of experimental estimates for model parameters. The initial values were chosen to enable simulations across a parameter range that demonstrates the model's potential to describe mechanisms modulating wing polyphenism in aphids. On the other hand, growth rate estimates were obtained experimentally (Carvalho et al. 2025) under scenarios designed to assess plant-specific effects on aphid repellency. Furthermore, the attack rate and predator conversion efficiency parameters were analyzed using parametric sensitivity analysis via bifurcation diagrams, with the aim of exploring the parameter space associated with predator-induced polyphenism.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

AI was employed to identify errors in computational code.

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Author contributions

Conceptualization: WACG. Formal analysis: WACG. Supervision: WACG. Validation: WACG.

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Data availability

All of the data that support the findings of this study are available in the main text.

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